Causes and consequences of age-assortative pairing in pied flycatchers (*Ficedula hypoleuca*)

Jaime Potti

Departamento de Biología Animal, Universidad de Alcalá, E-28871 Alcalá de Henares, Madrid, Spain.
e-mail: jaime.potti@uah.es

Abstract. This paper investigates patterns of age-related variation among pairs in a Spanish population of pied flycatchers (Aves: Muscicapidae**)** studied over a five-year period. Ages of birds in the sample ranged from one to seven years. Pairs formed at random with respect to size and body condition but age-based assortative mating was significant. Earliest breeding dates were observed in older (≥ 2 years) individuals, followed by mixed-age pairs, while younger pairs bred at later dates. However, when variation in breeding dates in relation to age of pair members was taken into account, quantity (number of recruits) and quality (size, body condition) of young did not differ among pairs of diverse age composition, although pairs composed of very old males and young females had fledglings with a lower weight. No positive evidence that age-assortative bonds were caused by active mate choice for absolute male age was found. However, the within-female repeatability of the absolute differences between her age and that of her mates was significant, indicating that the age difference between pairs may be a criterion for mate choice. Experimental studies are needed to determine whether age-assortative bonds and consistency of age differences between a female and her mates are caused by similar age-related patterns of arrival from spring migration in both sexes, or whether they are due to mate choice. Overall, the age of the pair did not play a significant role in the reproductive success of individual pied flycatchers, but showed a strong influence on arrival dates and onset of breeding. Variation in individual quality and high variance in reproductive success may override any fitness benefit resulting from pairing with older more experienced birds. In addition**,** age-assortative mating patterns in this population do not appear to alter the process of sexual selection based on variation among males in the expression of secondary sex ornaments.
Key-words: assortative mating, age, mating preferences, breeding time, fitness, passerines.

Resumen. *Causas y consecuencias del apareamiento concordante en papamoscas cerrojillos (*Ficedula hypoleuca*).* Se documenta el patrón de apareamientos en función de la edad en una población reproductora de papamoscas cerrojillos (Aves: Muscicapidae) estudiada durante cinco años y se indaga en las causas y en las consecuencias reproductivas de las diferentes combinaciones de edad entre ambos miembros de la pareja. Las edades de los individuos en esta muestra variaron desde uno a siete años. Las parejas se formaron al azar con respecto al tamaño o condición corporal, pero existió apareamiento concordante basado en la edad, es decir, los individuos se emparejaron con otros de edad igual o similar. Aunque las hembras no fueron consistentes en cuanto a la edad de los machos con los que se emparejaron en diferentes años, sí lo fueron en la diferencia de edades con respecto a sus parejas, indicando que éste podría ser un criterio en la elección de pareja. Son necesarios estudios experimentales para distinguir si los vínculos concordantes por edades dentro de la pareja se deben a elección activa por parte de los individuos o a patrones de llegada de la migración primaveral similares en ambos sexos. Las parejas formadas por individuos que tenían dos o más años tuvieron las fechas de cría más tempranas, seguidas por aquellas formadas por un individuo joven y el otro adulto, mientras que las parejas en que ambos individuos eran jóvenes fueron las que iniciaron la reproducción en fechas más tardías. Sin embargo, la cantidad y calidad de la descendencia, medidas como número de reclutamientos a la población reproductora y tamaño y condición corporal antes de la emancipación, respectivamente, no variaron en función de la composición por edades de la pareja una vez que se controló el fuerte efecto que tiene la edad individual sobre la fecha de cría en ambos sexos. Una excepción a este hecho fue que las parejas formadas por machos mucho más viejos que sus hem-

bras tuvieron nidadas de un menor peso antes de la emancipación. La edad del otro miembro de la pareja no fue en general importante, por tanto, para el éxito reproductivo de los papamoscas cerrojillos que, sin embargo, muestran una fuerte variación individual en dicho éxito con su propia edad. En la población estudiada, la variación independiente de la edad en la calidad individual y una alta varianza en el éxito reproductivo parecen compensar cualquier beneficio en eficacia biológica derivado del apareamiento con individuos adultos y experimentados. Tampoco se observa que el apareamiento concordante según edades pueda ser capaz de influir en las estimas de selección sexual basada en sendos ornamentos del plumaje masculino en esta especie.

Introduction

Much evidence has accumulated in recent years on the existence of mating preferences in many bird species (Andersson, 1994; Gibson & Langen, 1996). In European flycatchers of the genus *Ficedula* these preferences take the form of females favouring better territories (e.g. Alatalo et al., 1986; Slagsvold, 1986) and/or greater size and quality of expression of secondary male sexual traits (Røskaft & Järvi, 1983; Potti & Montalvo, 1991a; Sætre et al., 1994, 1995; Dale & Slagsvold, 1996; Sheldon et al., 1997). Ultimately, mating preferences may direct and constrain the rate of evolution of preferred traits (Andersson, 1994; Møller, 1994a). Furthermore, both these types of preferences may be based on, as well as constrained by, several factors, such as sensory biases (Ryan, 1997), search costs for prospecting females (Alatalo et al., 1988; Slagsvold et al., 1988), sexual imprinting (ten Cate & Bateson, 1988), or partner's age. Mate preferences apparently based on age are known in some birds species, originating positive age-assortative mating, i.e. birds of about the same age are more likely to become paired. Age-assortative mating may be a by-product of size-assortative pairing, having its basis, for example, on spatially widespread environmental effects on structural size across cohorts (e.g. Cooke et al., 1995), or may be due to cohort-independent preferences of birds of one sex for partners of a particular age (Cezilly et al., 1997). Assortative mating on the basis of age or experience has thus been mostly reported in long-lived birds and may be adaptive under some circumstances, e.g. due to increased reproductive success with age (Bradley et al., 1995). Among relatively short-lived passerines assortative mating on the basis of age has been documented more rarely (Berndt & Sternberg, 1971; Hund & Prinzinger, 1985) although it is probably widespread (Martin, 1985). In addition, as age-dependence also commonly occurs across a number of passerine life history stages (laying date, clutch size, hatching success, number of fledglings raised; Sæther, 1990; Martin, 1995), age-assortative pair bonds may also have consequences for reproductive success of individuals in relatively short-lived, passerine species.

In this paper, age-related patterns of assortative mating in a Spanish population of pied flycatchers *Ficedula hypoleuca* studied for five years are documented. In a previous study, Harvey et al. (1984) reported that egg-laying occurred earlier in pairs of pied flycatchers in which the male and female had bred previously than in pairs in which one or both parents were breeding for the first time. Timing of breeding has a large influence on the reproductive success of this species (Lundberg & Alatalo, 1992). Therefore, whether or not the observed age-related variation in pair bonds has a bearing on reproductive success, i.e. whether breeding time is taken into account, pairs of different age composition differ as to the quantity (number of recruited young) and quality (size, condition) of the offspring they raise is also examined. Finally, whether age-assortative bonds in the pied flycatcher, a model used in many studies of variation in secondary sex ornaments and sexual selection (Lundberg & Alatalo, 1992; Andersson, 1994; Dale et al., 1999), may bias the patterns observed as to mating preferences based on male secondary sex traits in this population (Potti & Montalvo, 1991a,b; Potti & Merino, 1996) is also addressed.

Material and Methods

A population of pied flycatchers breeding in nestboxes in an oak forest in La Hiruela, central Spain was studied from 1987 to 1992, with data on bird age being known from earlier studies started in 1984 (Potti, 1999a). Few data on male age were taken in 1990 due to a heavy episode of nest predation by weasels (*Mustela nivalis*) and this year was excluded from analyses. The birds were caught inside their nest boxes during incubation (females) or while feeding nestlings (males). Upon capture, all birds were aged as either yearling or older (Karlsson et al., 1986; Potti & Montalvo, 1991a), measured for wing and tarsus lengths and weighed (Potti, 1999a). A condition index was calculated for each bird as the residual of the regression of weight on tarsus length. Immigrant birds aged as older at first capture were assigned a minimum age of two years on the basis of evidence on age at first breeding of marked nestlings (Potti & Montalvo, 1991b). The data set thus consisted of birds aged 1-7 years (table 1), many of which figure repeatedly in the calculations. A few rematings between birds that were paired in former years (Montalvo & Potti, 1992) were discarded. For most purposes, to comply with statistical assumptions and increase sample sizes for the older classes, birds aged 4 years or older were grouped together (see table 1). Additionally, for
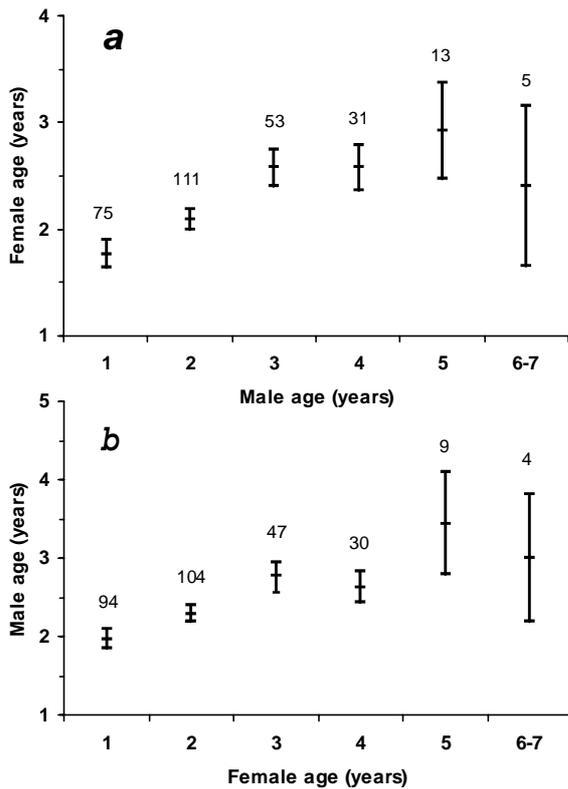
Figure 1.- Mean age (±S.E., in years) of individuals in relation to the age of their pair mates. Numbers are sample sizes.

Table 1. Age composition of the pied flycatcher population in 1987-1989 and 1991-1992. Figures show numbers of individuals in each age group, with the percentages of the total group in parentheses.

age (years)	males		females	
1	76	(0.26)	96	(0.33)
2	112	(0.38)	106	(0.36)
3	54	(0.19)	48	(0.16)
4	31	(0.11)	30	(0.10)
5	13	(0.04)	9	(0.03)
6	4	(0.01)	3	(0.01)
7	1	(0.003)	1	(0.003)

comparisons with earlier work on pied flycatchers (Harvey et al., 1984), birds were labelled as "young" when they were in their first calendar year while those labelled "older" were birds in their 2nd to 7th year. The laying date of a particular nest was defined as the day the first egg in the clutch was laid. Laying dates and numbers of recruits varied across years and were standardized by using the deviations of individual values from median annual values (laying date). The number of recruits was not normally distributed and transformations did not improve fits to normal distributions. New recruits were therefore classified into three classes (0, 1 or > 1 recruited young) and variation with their parents' ages was analyzed with log-linear analyses of frequencies. A low degree of polygyny (4%)was present in this population, with the offspring of secondary females suffering reduced growth and high mortality (Potti & Montalvo, 1993). To eliminate this source of variation, only monogamous pairs were considered.

The fledglings were ringed and measured for tarsus length and weight when they were 13 days old. As for adults birds, within-year condition indices were calculated for each individual fledgling. Recruitment of fledglings was followed until 1995. Nest averages of tarsus length, weight and body condition were used in the analyses. The role of different combinations of ages within pairs (table 2) was investigated by means of two-way ANOVAs, or ANCOVAs , taking seasonal trends with laying date as a covariate into account. The main focus of these analyses was to see whether different age combinations within pairs had a bearing on reproductive performance, i.e. testing the interaction term female age*male age, rather than main effects. To see whether the difference in ages (age difference hereafter) between pair members had any bearing on reproductive success and mate choice, male age was subtracted from female age within pairs.

Repeatability was used to analyze the consistency of female choice for male age and the age difference. To increase the power of analyses, an extended data set with repeated records of male age within individual females was used (see Potti, 1999a). Repeatability was estimated by making repeated (annual, in this case) measures of a sample of individuals and then calculating the ratio of the among-individual variance to the sum of both the among-individual and within-individual variances (the intraclass correlation coefficient, R; Zar, 1996). Components of variance were estimated by one-way ANOVA. A high repeatability indicated that variation within individuals was much smaller than among individuals. When measurements within individuals were very different, repeatability was low.

Sample sizes differ slightly among analyses because not all data could be taken for all individuals. Statistics (Zar, 1996) were two-tailed.

Results

Size and age composition of pied flycatcher pairs

Pair mates did not resemble each other in tarsus length (r=0.03, N=282, p=0.59), wing length (r=0.04, N=283, p= 0.51), weight (r=0.05, N=237, p=0.44) or body condition (r=0.02, N=237, p=0.71). The same is true if instead of using female weight taken during the incubation stage (when females are heaviest; Lundberg & Alatalo, 1992) weights recorded while feeding nestlings were used (Potti and Merino, 1995a). Thus, there was no evidence for assortative mating on the basis of these measurements of body size and condition.

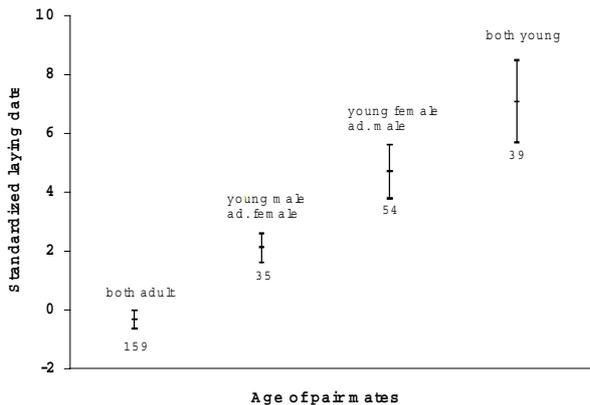Partners raw ages were associated across the five study years (Kendall's tau, t=0.26, N=288 pairs, p<

Figure 2.- Laying date (mean ± S.E.) of pied flycatchers as a function of the age (younger *vs* adult) of both pair members. Figures below bars are numbers of pairs.

0.0001; table 2). The same was true separately for each year, although the trend was only significant, or marginally so, in 1989 (t=0.39, p=0.0002), 1991 (t=0.27, p=0.01) and 1988 (t=0.23, p=0.06; 1987: t=0.19, p=0.23; 1992: t=0.09, p=0.34). The most frequent age combinations were pairs composed by yearlings and pairs formed by both individuals being in their second year. Later in life, birds in both sexes paired with birds of about the same age or younger so that very old birds tended to be paired with younger partners. This was more evident when illustrated across the entire range of actual ages (fig. 1). The age difference between pair members in this sample ranged from -5 to 5 years, with a mean (0.15, S.E.= 0.85 years) that did not deviate significantly from 0 (one sample t-test, t=1.75, N=288, p= 0.08).

Fitness consequences of pair-age combinations

Different pair-age combinations differed as to their onset of breeding (fig. 2). The earliest pairs were composed of older birds and the latest by the youngest age group in both sexes. For mixed-age pairs, the relative order of pair bond formation reflects the fact that some younger males settle from spring migration and pair before some older birds (Potti & Montalvo, 1991a).

Due to variations in breeding dates, differential success might accrue to pairs differing in age composition. However, when controlling for breeding date, the hypothesis that pairs differing in age composition should differ as to the quality or quantity of their offspring was rejected. Pairs with different age composition did not differ in any of the variables of growth of their young as scored at 13 days of age (table 3), after controlling for significant environmental (laying date, study year) and genetic (e.g. parents' tarsi; Alatalo & Lundberg, 1986) effects by means of ANCOVAs (all p>0.05 for the interaction term between male and female ages; table 3). The same conclusion was reached when individual ages were coded in two classes (yearling *vs* older; Harvey et al., 1984; all p>0.05). Neither did the categorised number

Table 2. Cross-tabulation of age (in years) in members of pied flycatcher pairs in 1987-1989 and 1991-1992. Figures show numbers of pairs in each age group.

	male age	1	2	3	≥4
female age	1	40	22	7	6
	2	33	50	14	14
	3	11	17	13	12
	≥4	10	15	13	11

of recruits vary across the different combinations of parents' ages (G^2=23.85, d.f.=18, p=0.16). However, the mass of nestling pied flycatchers varied in relation to the age difference between their parent's ages ($F_{7, 278}$= 2.67, p=0.01). Tukey *a posteriori* test revealed that this result was exclusively due to the fact that pairs formed by males much older (3-5 years older) than their mates had lower weight broods. This was not the case for either the number of fledglings raised ($F_{7, 287}$=0.78, p=0.61) or the mean within-brood tarsus length ($F_{7, 280}$=1.52, p=0.16). Neither did the categorised number of recruits (χ_7^2=16.23, p=0.30) or the chance of recruiting at least one young (χ_7^2=11.28, p=0.13) vary with the age difference between pair mates.

Female age, male secondary sexual traits and male age

Females differing in age did not vary as to their propensity to pair with males differing in mantle colour ($F_{3, 285}$=0.47, p=0.70) or the size of their pair's white forehead patch ($F_{3, 284}$=0.44, p=0.72). Thus, there was no evidence of variation in mate preferences on the basis of male ornaments respect to female age. Male age itself was not consistent within individual females throughout their lifetime breeding attempts (repeatability of male age within females, R=0.02; $F_{149, 368}$=1.06, p=0.35). However, the within-female repeatability of the absolute difference between her age and that of her mates was significant (R=0.20; $F_{146,362}$=1.63, p<0.001) indicating that females tend to be consistently younger, older or of about the same age as their (different) mates.

Discussion

While no evidence for assortative mating based on size or body condition was found in this study, pied flycatchers mated assortatively by age. The most frequent age combinations were pairs formed by birds in their second year and by yearlings, and the older the birds the higher was the probability of them becoming paired to younger birds. Was this a mere consequence of the scarcity of pairs of the same age as birds age, due to mortality?

Theoretically, this question could be answered by calculating expected mating frequencies between birds of different ages on the basis of age composition in the population (Berndt & Sternberg, 1971; Bradley

Table 3. Results of ANCOVAs testing for the effect of male and female ages and their interaction on number of offspring and measurements of growth recorded just before fledging. The analyses took significant variation with breeding date into account in all variables by using laying date as a covariate. Analysis of tarsus length included the midparent value to take into account significant genetic effects. The F statistics, degrees of freedom and associated probabilities are shown.

Variable	Effect	F	d.f.	P
Fledgling tarsus length (mm)	male age	2.30	3, 280	0.078
	female age	3.63	3, 280	0.014
	interaction	1.54	9, 280	0.136
Fledgling mass (g)	male age	1.52	3, 286	0.209
	female age	1.19	3, 286	0.314
	interaction	1.65	9, 286	0.118
Brood size	male age	0.59	3, 287	0.623
	female age	1.87	3, 287	0.315
	interaction	1.12	9, 287	0.346

et al., 1995). However, in a migrant species like the pied flycatcher a proper test of age-based mating preferences should take into account the availability of partners of a given age in a definite, finite "time window" spanning from settlement from migration and beginning of mate searching to mate choice. To do this, one should have data on the availability of different mates in the period between settlement and date of pairing (e.g. Møller, 1994b; Dale & Slagsvold, 1996). Such data are not available because female arrival dates are unknown and can only be approximated by pairing or laying dates which are not useful in this context. However, this may not be necessary since evidence suggests that absolute male age is not a focus of female choice. For example, male age itself was not consistent within individual females during their lifetime breeding attempts, indicating that females probably do not choose males on the basis of age. However, it may be that the absence of consistency in male age-based female choice is due to the fact that females age concurrently to them and may prefer mates of the same age or older, thus eliminating any repeatability of mate choice according to age.

From this viewpoint, the criterion for mate choice may be not a certain age but a certain age in relation to one's own age. The within-female repeatability of the absolute difference between a female's age and that of her mates was significant, even if low, indicating that the age difference between pair mates may be a criterion for mate choice. This intriguing result casts doubt on whether age-assortative bonds in the pied flycatcher are caused by active mate choice or due to similar age-related patterns of arrival from spring migration in both sexes (Potti, 1998; 1999b). The fact that most birds of a given age in both sexes arrive at similar times, with some overlap (Potti & Montalvo, 1991a), offers an opportunity for assortative-age pairing without any specifically selective activity during pairing, so that individuals simply take the next available partner (Bradley et al., 1995). In fact, age-assortative pairing was not significant in some years, for instance in 1988 when arrival dates were delayed

due to bad weather and a high overlap between sexes and ages occurred (Potti & Montalvo, 1991a). Similarly, the female consistency in the age difference between pair mates may also be due to a combination of significant consistency in female pairing and laying dates (Potti 1999b) and the age and sex-related patterns of arrival from spring migration (also see below). While data here reported cannot distinguish among alternative hypotheses, namely active choice or artefact due to other causes, these results suggest that taking into account age differences between pair mates in experimental tests of age-based mate choice (e.g. by means of choice tests in captivity; Slagsvold & Drevon, 1999) may be a promising research avenue.

Results herein do not lend support to the hypothesis of Sætre et al. (1994) who suggested that female pied flycatchers may benefit from choosing older (brighter) males over young, duller individuals because the former bring more food to the brood. If this were the case in the present population, pairs composed of experienced birds would be expected to have the highest quality broods, as expressed by their growth and condition, and produce more recruits. However, variation in age-mating patterns *per se* seemed to be neutral for the pair's reproductive fitness in our population, and the same was observed by Harvey et al. (1984) in a British population of pied flycatchers. This implies that, notwithstanding significant changes in reproductive performance with age in both sexes of the pied flycatcher (fig. 2; Lundberg & Alatalo, 1992; Sanz & Moreno, 2000), the annual reproductive success of individuals did not vary with their mate's age (see also Wheelwright & Schultz, 1994; Martin, 1995). Individuals in "mixed-age pairs" may be able to compensate for decreased performance of the other pair member due to lack of breeding experience, senescence (Pärt et al., 1992), or disease. Alternatively, pair members at any age may not be willing to compensate for a decreased parental effort by its pair and concomitant costs are paid by the offspring (e.g. Moreno et al., 1999). At any rate, the importance of an individual's own age in shaping patterns of variation

in reproductive performance in birds, including the pied flycatcher (Lundberg & Alatalo, 1992) can hardly be overemphasized (Martin, 1995). For example, age of individuals is one of the more pervasive correlates of female fecundity (Newton, 1990; Sæther, 1990; Desrochers & Magrath, 1993). Age is also a major determinant of performance in other contexts. For instance, many migratory birds arrive at the breeding quarters earlier as they grow older, with yearling, inexperienced birds being the last to settle and breed (Francis & Cooke, 1986; Hill, 1989; Lozano et al., 1996; Potti, 1998). In many bird populations there exists a strong selective pressure for breeding early as late breeders reach near zero fitness (Svensson, 1997; but see Brown & Brown, 2000). In addition, this selection pressure applies to both sexes for different related and unrelated causes. The possibility of acquiring better nests and territories (Alatalo et al., 1986; Slagsvold, 1986), high quality mates, as expressed by their resistance to trypanosome infection (Potti & Merino, 1996, and unpublished work), and a higher chance to become polygynous (Potti & Montalvo, 1993) are further benefits of an early arrival for males. Early females, on the other hand, rarely suffer costs from their increased likelihood of becoming involved in polygynous matings, as primary females in this population (whatever their age), enjoy the same success as monogamous ones. However, in spite of all these presumptive advantages of ageing, results reported here suggest that the age of a mate is not a main factor in determining reproductive success, at least in this population. Age-independent variation in individual quality, which is widespread (Clutton-Brock, 1988; Newton, 1990), and high variance in reproductive success combined with a relatively short life span (Sætre et al., 1994), as well as eventual compensation of decreased parental effort by the mate (Wright & Cuthill, 1990a,b) may override any effect of joint variation in age composition among pairs concerning reproductive success of pied flycatchers. Decreased parental effort by males paired to females much younger than themselves may also explain why these females had fledglings of a lower weight, and this could play a significant role in fledgling survival (Lindén et al. 1992). Similar findings were reported by Pärt et al. (1992), who found that males paired to very old females apparently capitalised on their mate's increased parental effort by reducing their own investment.

Unlike findings in northern, Scandinavian populations (Lundberg & Alatalo, 1992; Dale et al., 1999) and similar to the related Collared Flycatcher (*Ficedula albicollis*; Sheldon et al., 1997), female pied flycatchers in our southern population may base their mate choice on male territory (nest) quality and size of the male white forehead patch (Potti & Montalvo, 1991; Potti & Merino, 1996). Could age-assortative pairing mask estimates of sexual selection in the population studied? Age-assortative pairing, even if not based on active choice by individuals but due to similarity in patterns of arrival from migration in both sexes, might restrain the opportunity for sexual selection depending on the pattern of age-dependence of expression of sexual ornaments used in mate choice (Andersson, 1994). Conversely, age-assortative mating may also reinforce sexual selection if the expression of sexual traits is in fact age-dependent and related to fitness, imposing selection pressures on younger or poorer quality individuals expressing the trait to a lower degree. In the studied population of pied flycatchers, the expression of male mantle colour is slightly age-dependent, so that the mantle's plumage becomes blacker from the first to about the third year of life and then turns back to a browner colour type (Potti & Montalvo, 1991c; Potti & Merino, 1995b). However, females differing in age did not vary as to their propensity to pair with males differing in mantle colour. Neither did they differ as to the size of their pair's white forehead patch. The size of the male forehead patch remains rather constant throughout life, and shows no relationship with breeding date in the present population (J. Potti, unpubl. data), unlike the case in the related Collared Flycatcher *Ficedula albicollis* (Qvarnström, 1999). Interestingly, it has previously been shown that male and female pied flycatchers seem to pair assortatively with respect to the white patch on their forehead, which, in addition to all males, is also expressed in a fraction of older (≥ 2 years) females (Potti, 1993). Nevertheless, this relationship held irrespective of age in both sexes, and is thus independent of age-assortative pairing (Potti & Merino, 1996). As is the case for the white forehead patch, results herein also suggest that, if present, selection pressures on younger and older (i.e slightly browner) males to display a blacker plumage (Sætre et al., 1994) are not masked by age-assortative bonds in Spanish pied flycatchers.

References

Alatalo, R.V. & Lundberg, A., 1986. Heritability and selection on tarsus length in the pied flycatcher *Ficedula hypoleuca*. *Evolution*, 40:574-583.

Alatalo, R.V., Lundberg, A. & Ståhlbrandt, K., 1986. Female pied flycatchers choose territory quality and not male characteristics. *Nature*, 323:152-153.

Alatalo, R.V., Carlsson, A. & Lundberg, A., 1988. The search cost in mate choice of the pied flycatcher. *Anim. Behav.*, 36:289-291.

Andersson, M., 1994. *Sexual selection*. Princeton: Princeton University Press.

Berndt, R. & Sternberg, H., 1971. Paarbildung und Partnelalter beim Trauerschnäpper (*Ficedula hypoleuca*). *Vogelwarte*, 26. 136-142.

Bradley, J.S., Wooller, R.D. & Skira, I.J., 1995. The relationship of pair-bond formation and duration to reproductive success in short-tailed shearwaters *Puffinus tenuirostris. J. Anim. Ecol.*, 64: 31-38.

Brown, C.R. & Brown, M.B., 2000. Weather-mediated natural selection on arrival time in cliff swallows (*Petrochelidon pyrrhonota*). *Behav. Ecol. Sociobiol.*, 47: 339-345.

Cezilly, F., Boy, V., Tourenq, C.J. & Johnson, A.R., 1997. Age-assortative pairing in the greater flamingo *Phoenicopterus ruber roseus. Ibis*, 139: 331-336.

Cooke, F., Rockwell, R.F. & Lank, D.B., 1995. *The Snow Geese at La Pérouse Bay.* Oxford: Oxford University Press.

Dale, S. & Slagsvold, T., 1996. Mate choice on multiple cues, decision rules and sampling strategies in female pied flycatchers. *Behaviour*, 133: 903-944.

Dale, S., Slagsvold, T., Lampe, H.M. & Sætre, G.-P., 1999. Population divergence in sexual ornaments: the white forehead patch of Norwegian pied flycatchers is small and unsexy. *Evolution*, 53: 1235B1246.

Desrochers, A. & Magrath, R.D., 1993. Age-specific fecundity in European Blackbirds (*Turdus merula*): individual and population trends. *Auk*, 110:255-263.

Francis, C. M., & Cooke, F., 1986. Differential timing of spring migration in wood warblers. *Auk*, 103:548-556.

Gibson, R.M. & Langen, T.A., 1996. How do animals choose their mates? *Trends Ecol. Evol.*, 11: 468-470.

Harvey, P.H., Greenwood, P.J. & Campbell, B., 1984. Timing of laying by the pied flycatcher in relation to age of male and female parent. *Bird Study*, 31: 57-60.

Hill, G. E., 1989. Late spring arrival and dull nuptial plumage: aggression avoidance by yearling males? *Anim. Behav.*, 37:665-673.

Hund, K. & Prinzinger, R., 1985. Die Bedeutung des Lebensalters für brutbiologische Parameter der Mehlschwabe (*Delichon urbica*). *J. Orn.*, 126: 15-28.

Karlsson, L., Persson, K. & Walinder, G., 1986. Ageing and sexing in pied flycatchers *Ficedula hypoleuca* (In Swedish, with English summary). *Vår Fågelvärld*, 45:131-146.

Lindén, M., Gustafsson, L. & Pärt, T., 1992. Selection on fledging mass in the collared flycatcher and the great tit. *Ecology* 73:336-343.

Lozano, G. A., Perreault, S. & Lemon, R.E., 1996. Age, arrival date and reproductive success of male American Redstarts *Setophaga ruticilla. J. Avian Biol.*, 27:164-170.

Lundberg, A. & Alatalo, R.V., 1992. *The pied flycatcher*. London: T & A. D. Poyser.

Martin, K., 1995. Patterns and mechanisms for age-dependent reproduction and survival in birds. *Amer. Zool.*, 35: 340-348.

Møller, A.P., 1994a. *Sexual selection and the barn swallow*. Oxford: Oxford Univ. Press.

Møller, A.P., 1994b. Repeatability of mate choice in a monogamous swallow. *Anim. Behav.*, 47: 643-648.

Montalvo, S. & Potti, J., 1992. Breeding dispersal in Spanish pied flycatchers *Ficedula hypoleuca. Ornis Scand.*, 23: 491-498.

Moreno, J., Merino, S., Potti, J., de León, A. & Rodríguez, R., 1999. Maternal energy expenditure does not change with flight costs or food availability in the pied flycatcher (*Ficedula hypoleuca*): costs and benefits for nestlings. *Behav. Ecol. Sociobiol.*, 46: 244-251.

Pärt, T., Gustafsson, L. & Moreno, J., 1992. Terminal

investment and a sexual conflict in the collared flycatcher (*Ficedula albicollis*). *Am. Nat.*, 140:868-882.

Potti, J., 1993. A male trait expressed in female pied flycatchers *Ficedula hypoleuca*: the white forehead patch. *Anim. Behav.*, 45:1245-1247.

Potti, J., 1998. Arrival time from spring migration in male pied flycatchers *Ficedula hypoleuca*: individual consistency and familial resemblance. *Condor*, 100: 702-708.

Potti, J., 1999a. Maternal effects and the pervasive effect of nestling history on egg size in a passerine bird. *Evolution*, 53: 302-308.

Potti, J., 1999b. From mating to laying: genetic and environmental variation in mating dates and prelaying periods of female pied flycatchers *Ficedula hypoleuca. Ann. Zool. Fenn.*, 36: 187-194.

Potti, J. & Merino, S., 1995a. Female mass losses are related to male age and body condition in the pied flycatcher *Ficedula hypoleuca. Ardeola*, 42:173-181.

Potti, J. & Merino, S., 1995b. Some male pied flycatchers *Ficedula hypoleuca* in Iberia become collared with age. *Ibis*, 137: 405-409.

Potti, J. & Merino, S., 1996. Decreased levels of blood trypanosome infection correlate with female expression of a male secondary sexual trait: implications for sexual selection. *Proc. R. Soc. Lond. B*, 263:1199-1204.

Potti, J. & Montalvo, S., 1991a. Male arrival and female mate choice in pied flycatchers *Ficedula hypoleuca* in central Spain. *Ornis Scand.*, 22: 45-54.

Potti, J. & Montalvo, S., 1991b. Return rate, age at first breeding and natal dispersal of pied flycatchers *Ficedula hypoleuca* in Central Spain. *Ardea*, 79: 419-428.

Potti, J. & Montalvo, S., 1991c. Male colour variation in Spanish pied flycatchers *Ficedula hypoleuca. Ibis*, 133: 293-299.

Potti, J. & Montalvo, S., 1993. Polygyny in Spanish pied flycatchers *Ficedula hypoleuca. Bird Study*, 40: 31-37.

Qvarnström, A., 1999. Genotype-by-environment interactions in the determination of the size of a secondary sexual character in the collared flycatcher (*Ficedula albicollis*). *Evolution*, 53: 1654-1572.

Røskaft, E. & Järvi, T., 1983. Male plumage colour and mate choice of female pied flycatchers *Ficedula hypoleuca. Ibis*, 125: 396-400.

Ryan, M.J. 1997. Sexual selection and mate choice. In: *Behavioural ecology. An evolutionary approach*: 179-202 (Krebs, J.R & Davies, N.B., Eds.). Oxford: Blackwell Scientific Publications.

Sanz, J.J. & Moreno, J., 2000. Delayed senescence in a southern population of the pied flycatcher (*Ficedula hypoleuca*). *Écoscience*, 7: 25-31.

Sheldon, B.C., Merilä, J., Qvarnström, A., Gustafsson, L, & Ellegren, H., 1997. Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. *Proc. R. Soc. Lond. B.*, 264: 297-302.

Slagsvold, T., 1986. Nest settlement by the pied flycatcher. Does the female choose her mate for the quality of his house or himself? *Ornis Scand.*, 17: 210-220.

Slagsvold, T., & Drevon, T. 1999. Female pied flycatchers trade between male quality and mating status in mate choice. *Proc. Roy. Soc. Lond. B*, 266: 917-921.

Slagsvold, T., Stenmark, G. & Breiehagen, T., 1988. On the cost of searching for a mate in female pied flycatchers *Ficedula hypoleuca. Anim. Behav.*, 36: 433-442.

Svensson, E., 1997. Natural selection on avian breeding time: causality, fecundity-dependent, and fecundity-independent

selection. *Evolution*, 51: 1276-1283.

Sæther, B.-E., 1990. Age-specific variation in reproductive performance of birds. *Current Ornithol.*, 7:251-283.

Sætre, G.-P., Dale, S. & Slagsvold, T., 1994. Female pied flycatchers prefer brightly coloured males. *Anim. Behav.*, 48: 1407-1416.

Sætre, G.-P., Fossnes, T. & Slagsvold, T., 1995. Food provisioning in the pied flycatcher: do females gain direct benefits from choosing bright-coloured males? *J. Anim. Ecol.*, 64: 21-30.

ten Cate, C. & Bateson, P., 1988. Sexual selection: the evolution of conspicuous characteristics in birds by means of imprinting. *Evolution*, 42: 1355-1358.

Wheelwright, N.T. & Schultz, C.B., 1994. Age and reproduction in savannah sparrows and tree swallows. *J. Anim. Ecol.*, 36: 118-124.

Wright, J. & Cuthill, I., 1990a. Biparental care: short-term manipulation of partner contribution and brood size in the starling, *Sturnus vulgaris. Behav. Ecol.*, 1: 116-124.

Wright, J. & Cuthill, I., 1990b. Manipulation of sex differences in parental care: the effects of brood size. *Anim. Behav.*, 40: 462-471.

Zar, J. H., 1996. *Biostatistical analysis*. 3rd. Ed. Englewood Cliffs, NJ: Prentice Hall.